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Research Letters

Habitat fragmentation drives inter-population variation in dispersal behavior in a Neotropical rainforest bird

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ABSTRACT

Conservation ecology research, management and modeling often assume species-specific fixed traits ignoring intraspecific variation. Dispersal in animals is a heritable trait where intraspecific variation should be common, as it develops via interactions between landscape and behavioral processes. We conducted translocation-radio-tracking experiments and novel-environment tests on a Neotropical rainforest bird (*Pyriglena leucoptera*, Thamnophilidae) to assess whether dispersal success and exploratory behavior are determined by an individual's population of origin (i.e. fragmented or continuous forest). Based on a model for non-optimal animal movement in human-modified landscapes, we predicted that individuals that evolve or develop in fragmented landscapes, with daily exposure to risky boundary and matrix conditions, would have higher resistance to boundary-crossing and overall increased dispersal success than individuals from continuous habitats. We found that birds from fragmented landscapes were more resistant to cross boundaries and more successful at crossing the matrix relative to birds from continuous forest. Novel-environment tests detected reduced exploratory scores for birds from fragments, suggesting they were slower-explorers, and possibly more thorough in assessing their environment which, in turn, may have enabled more successful matrix transit. Observed behavioral differences can emerge by genetic adaptation or behavioral adjustments. In any case, because *P. leucoptera* is capable of adaptive behavioral adjustments to fragmentation, gradual landscape changes should be encouraged to minimize the potential for emergence of non-optimal dispersal behaviors in human-modified landscapes.

Introduction

Dispersal is a complex process involving the interaction between animal behavior and landscape structure (Baguette and Dyck, 2007). This is because landscapes in which organisms move are heterogeneous and composed of elements with dynamically changing costs and benefits for dispersing organisms (Belisle, 2005). Spatial models of animal distribution, commonly assume that dispersal strategies are fixed and evolutionarily stable. That is, individuals move according to species-specific decision rules, for example to avoid inbreeding or low suitability habitat (Lima and Zollner, 1996; Bonte et al., 2012). But dispersal is a complex and multi-phase life-history process that is under selection at each of its stages (Clobert et al., 2009) and, therefore, should rarely be invariant.

Sex-biased dispersal, for example, is a well-documented form of intraspecific behavioral variation (Pusey, 1987) and is commonly assumed to be a near-universal avian trait. Though, it is rarely considered in conservation planning, empirical study designs or in models of landscape connectivity. A recent study tested for sex-biased movement in an understory forest bird species in fragmented landscapes finding that males indeed had a reduced inter-patch movement success when compared to females (Awade et al., 2017). This finding confirms that sex-biased movements occur in fragmented landscapes, and should be more widely considered in connectivity-conservation scenarios; but also, that inter-individual variation in general should be considered. Given especially that dispersal behavior is heritable and under selection, differences among traits related to the different stages of dispersal (i.e., emigration, transfer in the matrix and immigration) should be expected among populations that persist in different landscape contexts (e.g., continuous or fragmented forests).

Indeed, organisms that persist in fragmented landscapes do exhibit inter-population variation in dispersal traits related to

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landscape structure. Butterfly populations from fragmented or disturbed habitats differ in dispersal related traits when compared to populations from continuous or undisturbed habitats (Merckx and Van Dyck, 2006; Öckinger and Van Dyck, 2012). In a long-term capture–recapture study of forest birds in Amazonia, conspecific individuals exhibited differences in maximum dispersed distances depending on whether they occurred in forest fragments or continuous forest (Van Houtan et al., 2007). Studies in temperate forests demonstrate that birds hatched in isolated territories have greater natal dispersal distances (Pasinelli et al., 2004) and a delay of dispersal events (Lens and Dhondt, 1994).

Fahrig (2007) proposed a conceptual model for dispersal evolution in different landscape contexts. The model predicts that individuals evolving in continuous habitats, with little or no experience with habitat boundaries, would exhibit low resistance to cross boundaries that they do encounter. In fragmented landscapes, those individuals experience high mortality in the matrix due to the usually high-risk matrix encountered after crossing a boundary, and therefore have generally low dispersal success, which makes them maladapted in human modified landscapes. On the other hand, in young birds from fragmented landscapes that developed exposed to a risky matrix and its boundary conditions, there should be strong selection for appropriate risk-averse movement decisions including behavioral avoidance of crossing dangerous habitat boundaries. This model assumes selection and genetic adaptation over longer time scales as the main driver of boundary responses but behavioral variation in the short term can also emerge by behavioral plasticity (Stamps and Biro, 2016).

Animals have the ability to change their behavior to reduce risk (Lima and Dill, 1990). During exploration and dispersal movements, risks to birds abound but the collection and use of information about those risks can make dispersal safer for individuals (Delgado et al., 2014). However, dispersing animals can only use information if they are able to correctly interpret available cues, for example those related to different kinds of predation threats (Huang et al., 2012). The capacity of using this information can be either inherited or obtained from direct experience with their environment (Spiegel and Crofoot, 2016). That is, movement behavior in fragmented landscapes might also emerge as some individuals adjust their movement behavior based on state-dependent conditions. For example, wild great tits (*Parus major*) became fast movers or fast explorers (i.e., exhibit increased risk taking behavior) when their probability of survival was experimentally decreased (Nicolaus et al., 2012).

Within birds and other vertebrates, exploratory behavior is a key trait underlying individual variation in use of space and resources because it provides the means to learn about and utilize the environment (Mettke-Hofmann et al., 2006). Thus, individuals that spend their juvenal exploratory phase in fragmented landscapes may be exposed to many different cues, information types and sources, and develop different decision-making strategies when compared to individuals that grow up in a continuous habitat without complex boundary conditions (Spiegel and Crofoot, 2016; Reader, 2015). Additionally, juvenal individuals that make poor decisions in gap and forest boundary crossing may get weeded out, leaving adults in fragmented habitat with better spatial decision-making regarding edges and their dangers (Cosentino and Droney, 2016).

We conducted a translocation experiment with radio-tracking to assess whether inter-patch dispersal success is different among individuals of populations belonging to contrasting landscapes (i.e. fragmented vs. continuous forest) in a Neotropical rainforest bird species, the White-shouldered Fire-eye (*Pyriglena leucoptera*, Thamnophillidae). Our main hypothesis, derived from Fahrig's (2007) framework and other empirical evidence reviewed above, is that lack of previous experience with a fragmented landscape should hinder successful inter-patch movement in White-shouldered Fire-eyes raised in continuous unbroken forest (and vice versa; birds living in fragmented habitat would disperse better in a fragmented landscape). Furthermore, we propose that this pattern is a consequence of higher emigration propensity in edge-naïve birds from continuous forest (i.e. low resistance to cross boundaries) with higher mortality in the matrix, while individuals from the fragmented landscape should show lower emigration propensity (i.e. high resistance to cross boundaries) but an overall higher dispersal success because once they leave a fragment they are more successful crossing the matrix. To help reveal differences in emigration propensity, we subjected birds to a short behavioral trial in a cage to determine their location on the fast-slow exploratory continuum, because there seems to be a correlation between 'slow' exploring in birds and higher survival in the face of risky decision-making (Hall et al., 2015).

Therefore, our specific predictions are as follows: individuals from fragmented landscapes (i) should take longer to leave a small forest patch, (ii) spend less time crossing matrix habitat when moving (thereby minimizing exposure to predators) and, consequently, (iii) exhibit greater success in arriving to a neighboring forest patch and, finally, in the behavioral trials, (iv) birds from the fragmented landscape should be slower explorers than birds raised in continuous forest. Our study design cannot disentangle selective genetic change from behavioral adjustments, but rather aims to test whether inter-population variation in dispersal traits can arise in response to human-driven landscape change. We also seek to provide information for better management practices to enhance connectivity in fragmented landscapes.

Methods

Study site and model species

We conducted this study in the sub-tropical Atlantic Forest region located in the Atlantic Plateau of São Paulo, southeastern Brazil (47° 20′ W–48° 40′ W and 23° 43′ S–24° 06′ S). The area encompasses a fragmented landscape (ca. 30% forest cover) dominated by small habitat patches of secondary forest (<100 ha) embedded in a matrix dominated by croplands and pastures (>80% of the matrix). The fragmented landscape is adjacent to a large protected forested area (>1,000,000 ha of continuous forest; Ribeiro et al., 2009).

The White-shouldered Fire-eye (*P. leucoptera*, Thamnophillidae) is an endemic bird of the Atlantic Forest found in the understory of primary and secondary forests and frequently close to edges in forest fragments (Hansbauer et al., 2007, 2008a,b; Sick, 1997). It is a 30 g insectivorous bird with marked sexual dimorphism that forages while following army-ants (Sick, 1997). We selected this species because it is common in fragmented landscapes where forest cover exceeds 30%, but uncommon or absent where less than 15% forest cover remains (Boscolo and Metzger, 2011). It is not endangered and was categorized with medium sensitivity to landscape change (Hansbauer et al., 2008a; Uezu et al., 2005).

Experimental design

We used a translocation-and-radiotracking experimental design similar to that utilized by Castellón and Sieving (2006) and we followed the same field protocol as Awade et al. (2017). Birds were captured in continuous forest sites (>1,000,000 ha) or in fragmented landscape sites and then released in forest patches located >10 km away in the fragmented landscape. This design simulates a situation analogous to a characteristic phase of dispersal; that is, having to move through an unknown area with